

A PLIOCENE URSID FROM SOUTH AFRICA

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(With plates 19–20, 2 figs and 3 tables)

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INTRODUCTION

There are few mammal-bearing deposits of Pliocene age known in Africa (Kurtén 1971: 134) and consequently occurrences which date from this epoch are of significance in that they may produce records of species which are of special phylogenetic and zoogeographic interest. The only Pliocene occurrences presently being investigated in southern Africa are those at Langebaanweg in the Cape Province (Hendey 1970a, 1970b), and one of the more remarkable records from this locality is that of an agriotheriine ursid (Hendey 1969). It was the first record of an agriotheriine in Africa, and is still the only ursid known from sub-Saharan Africa.

The Agriotheriinae, which in the most restricted sense may be taken to include the genera *Agriotherium* and *Indarctos*, are known from a number of late Tertiary and early Pleistocene occurrences in Eurasia and North America, and the South African record adds a new dimension to concepts of the evolution and dispersal of this group. In general, the recorded species are represented by rather fragmentary material and, unfortunately, this is also the case with the Langebaanweg form. However, the significance of the material is not diminished, although the description which follows might well require revision if more specimens are recovered in the future.

The terrestrial mammal fauna with which the Langebaanweg agriotheriine is associated includes a number of species which are unexpected in an African context. For example, one of the hyaenids is referred to *Percrocuta*, a genus which is otherwise known in Africa only from the Algerian Miocene (Thenius

1966). It was, however, widely distributed in Eurasia during the late Tertiary (Kurtén 1957a). A second unusual species is an as yet unnamed boselaphine antelope, which apparently derives from the Miocene *Protragocerus labidotus* of Kenya (Gentry 1970). The boselaphines were also common in Eurasia during the late Tertiary.

Other significant, although not unexpected, records from Langebaanweg include an early ancestor of *Hyaena hyaena*, a primitive form of *Mammuthus subplanifrons* which is one of the earliest of the true elephants (Maglio & Hendeby 1970), and an ancestor of the white rhinoceros, *Ceratotherium simum* (Hooijer, in press).

The Langebaanweg deposits are unique amongst the major late Cenozoic fossiliferous occurrences of sub-Saharan Africa in that a marine fauna is associated with the terrestrial vertebrate fossils. Vertebrates linked with the marine environment include the first recorded fossil penguin from Africa (Simpson 1971) and an unusual monachine seal, *Prionodelphis capensis* (Hendeby & Repenning 1972), which has shed some light on the origins of the Antarctic seals (Hendeby 1972).

Viewed in relation to the fauna as a whole, the agriotheriine is but one of a series of important additions to the fossil record of the late Cenozoic of Africa.

In order that this species might be placed in taxonomic perspective, its description is preceded by a brief review of the Ursidae.

THE FAMILY URSIDAE

The Ursidae are a comparatively recently evolved mammalian group, with a relatively small number of constituent genera, and they have received a considerable amount of attention from palaeontologists and neontologists alike. Despite this they have proved an extremely controversial group and it is only recently that a measure of agreement has been reached on their phyletic and intra-familial relationships.

The most comprehensive account of the Ursidae is that of Erdbrink (1953), and this has provided an invaluable basis for more recent work on the family. Since the appearance of Erdbrink's monograph much attention has been focused upon the ursine bears (the genus *Ursus* and closely related forms). Their phylogeny is now one of the best known of all mammalian groups and this successful study has been largely due to the work of Kurtén (1957b, 1958, 1964, etc.) and Thenius (1959a). Much the same can be said of the tremarctine bears (the genus *Tremarctos* and its close relatives) (Kurtén 1966, 1967), although the origin of this group remains obscure.

The taxonomic position of the giant panda, *Ailuropoda melanoleuca*, has been a matter of controversy for more than a century owing to its combination of ursid and procyonid characteristics. Davis (1964) presented what is perhaps the definitive study of the anatomy of this animal, and he held the view that it is indeed a bear. While this conclusion is still not universally accepted, *Ailuropoda* is regarded as an ursid in the present study.

The Tertiary ursids, excluding the immediate ancestors of the ursine group, can conveniently be placed in two categories. The first includes those genera which bridge the evolutionary gap between the Canidae and 'true' bears. They are *Cephalogale*, *Hemicyon* and *Dinocyon*. Secondly, there is a more advanced group in which many specialized ursid characteristics were developed. This group includes *Agriotherium* and *Indarctos*. Not surprisingly these two groups may be broadly differentiated on temporal as well as morphological grounds, the former being essentially Miocene in age, and the latter dating largely from the Pliocene. The Tertiary ursids are not as well known as the Quaternary forms because they are less well represented in the fossil record. There are also many uncertainties regarding the relative ages of some members of the groups.

Frick (1926) separated these Tertiary forms from both the Canidae and Ursidae, placing them in a single unit which he called 'Hemicyoninae'. Subsequently Pilgrim (1932) referred them all to the Ursidae and this arrangement is generally followed today.

There have been many differences of opinion concerning formal subdivisions within the family. For example, Kraglievich (1926) proposed separation into three subfamilies, which Simpson (1945: 225) argued was 'of very doubtful theoretical validity and of little or no practical convenience'. Indeed, he even appeared to be in some doubt as to whether the bears merited family rank. Erdbrink (1953) was another not in favour of having subfamilies within the Ursidae. Today it has become fairly widely accepted that subfamilial grouping is both reasonable and desirable and the arrangement usually followed is that of Thenius (1959a), who recognized the Hemicyoninae, Agriotheriinae, Tremarctinae and Ursinae.

In spite of the formal system of zoological nomenclature, there is a strong element of personal opinion in the definition of many taxa. The inclusion or exclusion of the Hemicyoninae from the Ursidae appears to depend largely upon whether a 'vertical' or 'horizontal' system of classification (Simpson 1945) is favoured. An excellent example of this basic difference in approach is afforded by the controversy which has surrounded the taxonomy of early Pleistocene Hominidae. Reed (1967) has given a concise summary of the two points of view, and states that 'as gaps in the fossil record . . . have been filled, the tendency has been . . . to shift from a horizontal (grade) type of classification to a vertical (clade) type'.

While the general pattern of ursid evolution has long been appreciated, the intra-familial groupings have tended to emphasize morphological rather than phylogenetic aspects of the family. An attempt has been made here to classify the ursids according to their phylogeny, although this was hampered by the fact that there are still certain critical points in ursid evolution which are not satisfactorily resolved. The intra-familial classification to be given presently follows that of Thenius (1959a), but is modified on the basis of the tentative phylogeny presented in Figure 1. This phylogeny is based on the work of

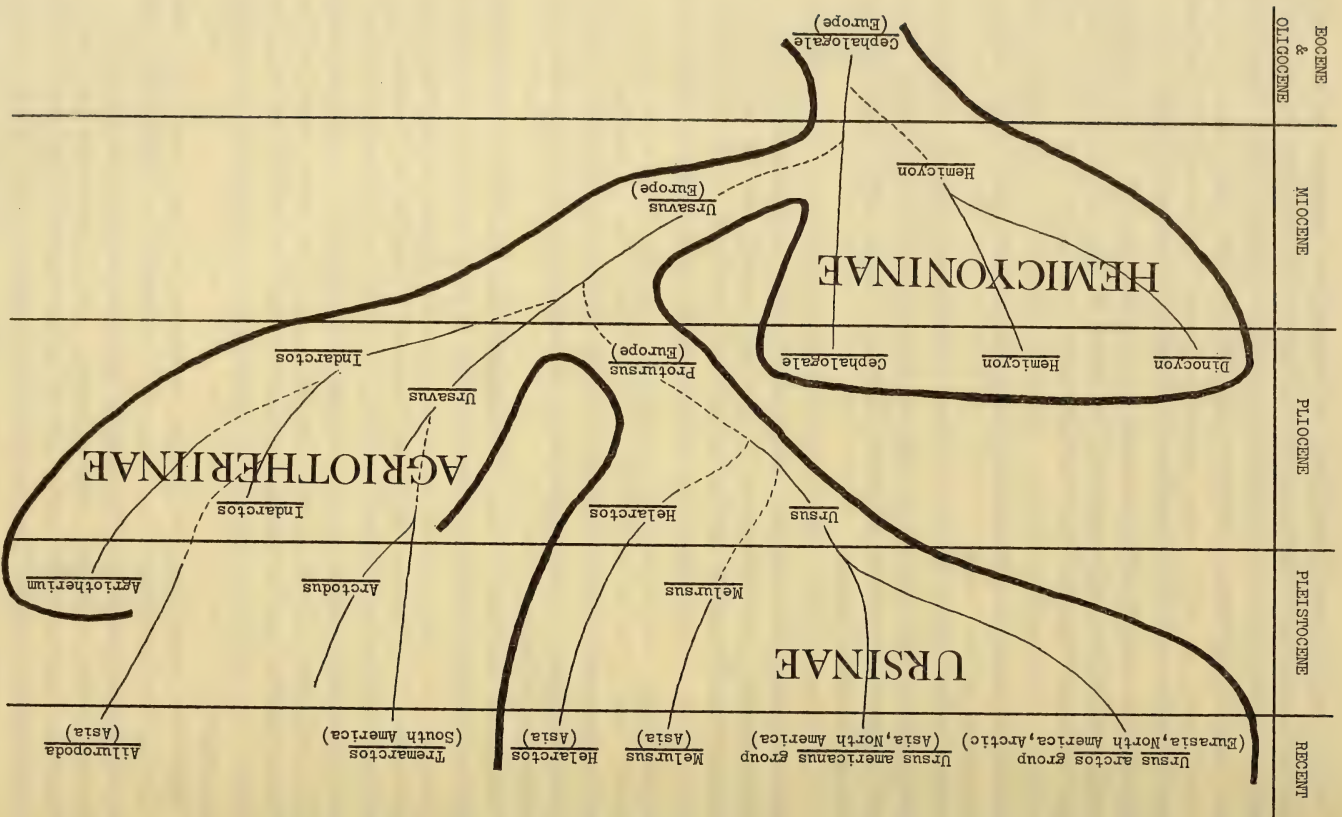


FIG. 1. Tentative phylogeny of the Ursidae.

Erdbrink, Kurtén and Thenius, and the morphological characters, temporal range and geographical distribution of each genus was taken into consideration.

The pattern which emerges is one of three distinct radiations within the family, each successive radiation cutting out the one preceding temporally and/or geographically. In each case the stem genus is recorded in Europe, and dispersals were largely confined to the northern continents. The intra-familial classification arrived at is as follows:

| <i>Subfamily</i> | <i>Tribe</i> | <i>Genera included</i> |
|-------------------|------------------|--|
| Hemicyoninae .. | Hemicyonini .. | <i>Cephalogale, Hemicyon, Dinocyon</i> |
| Agriotheriinae .. | Agriotheriini .. | <i>Ursavus, Indarctos, Agriotherium</i> |
| | Ailuropodini .. | <i>Ailuropoda</i> |
| | Tremarctini .. | <i>Arctodus, Tremarctos</i> |
| Ursinae | Ursini | <i>Protursus, Ursus, Helarctos, Melursus</i> |

The replacement of the Hemicyoninae by the Agriotheriinae, and the latter in turn by the Ursinae, can be accounted for in general by assuming that there was competition between better and lesser adapted groups. Such competition would, of course, have taken place at the species level, but would ultimately have been manifested in higher taxonomic categories as well.

Kurtén (1957c: 224) has concluded that the replacement of a species by an ecologically related species may occur in one of three ways:

- (1) 'The extinction of the earlier form has no causal connection with the immigration of the later form. Both result from the action of other factors, for instance climatic.'
- (2) 'The extinction of one species permits the subsequent immigration of another.'
- (3) 'The immigrating form is adaptively superior to the local form, and ousts it through competition.'

While the third alternative is the one concluded to be the most generally applicable in the present instance, it was almost certainly not the sole factor involved in the extinction of ursids. Furthermore, competition was probably not confined only to members of the family, and some ursids probably became extinct as a result of competition with members of other families. This might well have been the case with the somewhat aberrant ursid *Agriotherium*.

INTRA-FAMILIAL CATEGORIES WITHIN THE URSIDAE

Subfamily **Hemicyoninae**

Diagnosis (adapted from Pilgrim 1931). Ursidae with the upper profile of the skull almost rectilinear; snout relatively long and narrow; infra-orbital foramina rather remote from orbits; temporal fossae long and deep; occiput low; sagittal and lambdoidal crests prominent; zygomatic arches relatively narrow; P² and P³ double-rooted; P⁴ situated behind infra-orbital foramen,

and antero-posterior diameter equal to or slightly exceeding that of M^1 ; P^4 with prominent protocone situated towards the midpoint of the tooth, and parastyle absent; M^1 larger than M^2 , with the transverse diameter of these teeth exceeding antero-posterior diameter, and with internal cusps crescentic inwards; M^3 always absent; mandible with premaseteric fossa and full complement of teeth; P_2 to P_4 double-rooted; M_1 large with talonid becoming prominent; M_2 smaller than M_1 , double-rooted with antero-posterior diameter slightly greater than transverse diameter; M_3 small, single-rooted and slightly elongated antero-posteriorly; postcranial skeleton a cursorial type, feet digitigrade; humerus with entepicondylar foramen.

Discussion. In general there was an increase in body size with time, and some later Hemicyoninae were as large as the biggest of modern bears. Although probably carnivorous on the whole, at least one genus (*Cephalogale*) apparently became progressively more omnivorous, and it is regarded as the ancestor of all ursids.

Early in their history the Hemicyoninae were confined to the Old World and only spread to North America at the peak of their radiation in the late Miocene. Although they were a restricted group generically, they were widespread and apparently very successful in the northern continents during the Miocene. They became extinct early in the Pliocene when the radiation of the Agriotheriinae was beginning.

Subfamily **Agriotheriinae**

Tribe *Agriotheriini*

Diagnosis. Ursidae with the upper profile of the skull rather convex; snout fairly short and broad; infra-orbital foramina close to orbits; occiput moderately high; sagittal crest not prominent; zygomatic arches becoming broad; P^4 situated below or slightly anterior to infra-orbital foramen, with antero-posterior diameter approximately equal to that of M^1 ; P^4 protocone becoming progressively larger and sometimes with accessory cusps developed anterior to it; P^4 parastyle develops and becomes progressively larger; M^1 roughly square; M^2 sometimes with talon; M^3 always absent; mandible sometimes with premaseteric fossa; M_1 usually large and sectorial; M_2 elongated; M_3 usually circular or very slightly elongated; postcranial skeleton progressively more heavily built; humerus (usually) with entepicondylar foramen.

Tribe *Ailuropodini*

Diagnosis. Ursidae with upper profile of skull convex; snout short and broad; infra-orbital foramina close to orbits; sagittal crest not prominent; P^1 vestigial or absent; P^4 large with prominent protocone and antero-internal cusp (protocone lobe), and prominent parastyle; P^4 situated below infra-orbital foramen, with antero-posterior diameter slightly greater than that of M^1 ; M^1 roughly square with prominent internal cingulum; M^2 elongated with

prominent internal cingulum and talon on which multiple cusplets are developed; M^3 always absent; mandible without premaseteric fossa; P_1 vestigial; M_1 large, elongated and non-sectorial; M_2 large and slightly elongated with multiple cusplets on occlusal surface; postcranial skeleton robustly proportioned; non-cursorial; humerus with entepicondylar foramen.

Tribe *Tremarctini*

Diagnosis. Ursidae with the upper profile of the skull rather convex; snout relatively short and broad; infra-orbital foramina close to orbits; sagittal crest sometimes prominent; zygomatic arches moderately broad; P^4 situated anterior to infra-orbital foramen, with antero-posterior diameter usually less than that of M^1 ; P^4 protocone prominent and parastyle absent; M^1 roughly square or slightly elongated; M^2 elongated with prominent talon; M^3 always absent; mandible with premaseteric fossa; M_1 large, elongated and non-sectorial; M_2 elongated, antero-posterior diameter approximately equal to that of M_1 ; M_3 moderately large and slightly elongated; postcranial skeleton robustly proportioned; non-cursorial; humerus with entepicondylar foramen.

Discussion. As here defined the Agriotheriinae are the most diverse of the ursid subfamilies. It includes the genus *Ursavus* which is the earliest member of the family which is unmistakably 'bear-like', and which is regarded as the stem genus of the ursids by those who include the Hemicyoninae in the Canidae (e.g. Kurtén 1966). It is known only in Europe.

An apparent off-shoot from *Ursavus* was *Indarctos*, a genus which is first recorded in the early Pliocene of Europe. It is uncertain which species of *Indarctos* is the earliest. One possibility is *I. vireti* Villalta & Crusafont 1945 from Spain, while another is the agriotheriine from the lignites of Monte Bamboli in Italy (Erdbrink 1953). The transition from *Ursavus* to *Indarctos* appears to be principally a matter of an increase in size.

A number of other species of *Indarctos* have been recorded in the Pliocene of the northern continents. European species are *I. arctoides* Deperet 1895, *I. atticus* Dames 1883 and *I. ponticus* Kormos 1913, while *I. lagrelli* Zdansky 1924 is from China, *I. punjabensis* Lydekker 1884 from India and *I. oregonensis* Merriam *et al* 1916 from North America. In general the recorded specimens of *Indarctos* are rather fragmentary, and consequently definitions of the species are often inadequate. Pilgrim (1931) noted the similarity between *I. ponticus* and *I. lagrelli*, and Kurtén (1957*c*) regarded them as conspecific. Probably the recovery of additional material and a review of the genus would result in further synonymies being recognized.

Much the same can be said of *Agriotherium*, except that this genus survived into the Villafranchian of Europe (Kurtén, 1968), and as the new record from Langebaanweg shows (*vide infra*), it also became established in Africa. As far as could be determined there is no early Pliocene record of this genus. Species include *A. insigne* Gervais 1853 from Europe, *A. maraghanus* Mecquenien 1925

from Iran, *A. palaeindicus* Lydekker 1878 and *A. sivalensis* Falconer & Cautley 1836 from India, and *A. gregoryi* Frick 1921 from North America.

Probably the best published account of the differences between *Agriotherium* and *Indarctos* is that of Pilgrim (1932). He was apparently the first person to conclude that *Agriotherium* is the more advanced of the two genera, although only in some respects and he stated that *Indarctos* was a development from *Agriotherium*. This is a traditional point of view which is still widely held, and *Agriotherium* has often been referred to as a link between the Canidae and Ursidae.

The present study led to the conclusion that the characteristics of *Agriotherium* are not primitive, but rather the result of the development of specializations. *Agriotherium* is regarded as a derivative of *Indarctos* in which there was a trend towards the development of more carnivorous habits. The alternative view that *Indarctos* was derived from *Agriotherium* is rendered a little unlikely by the known temporal ranges of the two genera, and the possibility that both are descended from a hypothetical common ancestor is an unnecessary theory.

The general trend in ursid evolution has been towards the development of characters suited to an omnivorous or herbivorous diet. There is at least one well-documented reversal of this trend. The polar bear, *Ursus maritimus*, is a purely carnivorous form which still retains many of the characters of *U. arctos*, the species from which it is derived (Kurtén 1964). This anomalous development may have come about during one of the Pleistocene glaciations when an *U. arctos* population adapted to life in a vegetation-less peri-glacial environment. Since the dichotomy of *U. maritimus* and *U. arctos* took place comparatively recently, the dentitions of the two species are still essentially similar. Given sufficient time the *U. maritimus* dentition would become increasingly modified, with the carnassials developing at the expense of the molars.

Agriotherium was probably just such an exception to the general rule in ursid evolution, but in this instance the carnivorous habits are reflected by the nature of the dentition. The numerous references to its 'primitive' and 'canid-like' characteristics imply 'carnivore-like', which is not necessarily primitive at all. In fact Erdbrink (1953: 582) referred to the upper carnassial of *Agriotherium* as being 'very carnivorous in aspect'.

The most important characters which distinguish *Agriotherium* from *Indarctos* are to be found in the dentitions, and basically the differences are centred on the emphasis of the carnassials and the reduction of the other cheekteeth in *Agriotherium* (Pilgrim 1932: 42).

In *Agriotherium* the anterior premolars in both maxilla and mandible are reduced in size and sometimes number. This is not necessarily an indication of a carnivorous diet, since many ursines also have the anterior premolars reduced or lost, but in this group the molars are correspondingly enlarged and the reduction also affects the carnassials. This is not so in *Agriotherium*.

This genus differs from *Indarctos* in having the lingual margins of M¹ and M² shorter than buccal margins as a result of the paracones and metastyles

being more strongly developed than the protocones and hypocones. Since the buccal cusps are higher than lingual ones it is possible for them to act as shearing as well as crushing agents. The crushing function of the M^2 of *Indarctos* is further indicated by the presence of a talon, and in this genus the M^2 is always longer than M^1 . By contrast the M^2 of *Agriotherium* is nearly always smaller than M^1 and lacks the talon. Erdbrink's (1953: 571) conclusion that there is 'at best a beginning of a talon . . . in *A. insignis*' is probably incorrect, and the talon in this species is regarded as vestigial.

The 'carnivorous aspect' of the upper carnassial of *Agriotherium* has already been mentioned, and this tooth is also the most important in so far as the inferences on the ancestry of the genus are concerned. It is characterized by the presence of a prominent parastyle, a cusp which is not found in any of the Canidae, Hemicyoninae or species of *Ursavus*. It is, however, present but small in some species of *Indarctos* (e.g. *I. punjabiensis*). This suggests a progressive development of a P^4 parastyle in the Agriotheriinae as follows:

Ursavus (absent)—*Indarctos* (small)—*Agriotherium* (prominent).

In *Ailuropoda*, which is here regarded as another descendent of *Indarctos*, it is also prominent.

The lower carnassial of *Agriotherium* also exhibits 'carnivorous' characteristics. The talonid is reduced relative to the trigonid and the hypoconid is higher than the entoconid, which makes it a more efficient shearing tooth than that of *Indarctos*.

The reasons for the development of an apparently carnivorous lineage stemming from *Indarctos* are not known, but this might have been in response to competition with early Ursinae. By the late Pliocene when the ursine radiation was getting under way in Europe, *Agriotherium* was the only agriotheriine surviving in this area and it only became extinct in the early Pleistocene. It follows that if it was indeed a purely carnivorous form, its ultimate extinction in Europe and elsewhere cannot be explained in the same way as the extinction or limitation of other Agriotheriinae. In this instance competition with other fissiped carnivores may be the answer, although other undetermined factors might have been involved.

In the late Pliocene *Indarctos* was still present in Asia, an area in which the Ursinae had not yet become common, and it is only in Asia that *Ailuropoda* is recorded. Those authors who have accepted *Ailuropoda* as an ursid have invariably suggested its descent from the *Agriotherium/Indarctos* group (see Davis 1964), and *Indarctos* appears to be the only known fossil form from which *Ailuropoda* can be satisfactorily derived. Since *Ailuropoda* was well established early in the Pleistocene, and since it is a good deal more advanced than *Indarctos*, its differentiation must have taken place during the Pliocene, probably at about the time that *Indarctos* itself was nearing extinction.

Much of the controversy about the status of *Ailuropoda* seems to stem from the fact that it is almost always compared with modern ursine bears, from which it does indeed differ quite markedly. However, if it is taken into account

that their common ancestor was a Miocene form (Fig. 1), the differences are hardly surprising. The differences between the European early Pleistocene *Ursus minimus* and *Agriotherium insigne* are as great, or even greater, than those between modern ursines and *Ailuropoda*, yet the referral of *Agriotherium* to the Ursidae is no longer questioned.

In order to illustrate that on dental evidence alone *Indarctos* could be ancestral to both *Ailuropoda* and *Agriotherium*, a list of some characters of the upper cheekteeth of these three genera is given in Table 1. On the one hand the dentition is modified for a herbivorous diet (*Ailuropoda*), and on the other a carnivorous dentition is developed (*Agriotherium*).

TABLE 1. Some characters of the upper dentitions of *Ailuropoda*, *Indarctos* and *Agriotherium*.

| <i>Ailuropoda</i> | <i>Indarctos</i> | <i>Agriotherium</i> |
|---|--|---|
| Herbivorous lineage | Ancestral genus | Carnivorous lineage |
| <i>Anterior premolars</i> | | |
| P ¹ sometimes absent | P ¹ present | P ¹ present (?) |
| P ² & P ³ double-rooted | P ² & P ³ double-rooted in early forms (?) | P ² & P ³ single-rooted |
| <i>Carnassial</i> | | |
| P ⁴ with prominent parastyle and antero-internal cusp | P ⁴ parastyle absent or small, antero-internal cusp small | P ⁴ with prominent parastyle, antero-internal cusp usually absent |
| <i>Molars</i> | | |
| M ¹ square with prominent lingual cingulum, four main cusps and smaller cusplets | M ¹ square, four main cusps only | M ¹ narrower lingually, four main cusps only |
| M ² elongated with prominent talon, four main cusps and many cusplets | M ² slightly elongated with small talon and four main cusps | M ² nearly square, talon vestigial or absent, usually four main cusps only |

The range of *Ailuropoda* diminished considerably during the Quaternary and it now survives in a natural state only in isolated areas in China. During the Pleistocene it was widely distributed in China, and is also recorded from Burma (Smith-Woodward 1915). It was during the Pleistocene that the Asiatic radiation of the Ursinae took place and this suggests that *Ailuropoda* may have been an unsuccessful competitor with this group. It is therefore another agriotheriine whose decline is attributed to the Ursinae.

The decision to include the tremarctines in the Agriotheriinae is not easily justified. Superficially at least, there are similarities between the extant *Ailuropoda melanoleuca* and *Tremarctos ornatus*, and both differ from *Ursus*. There are resemblances in general skull morphology, both being 'short-faced' forms, and Davis (1955: 29) states that, 'Except for the pre-masseteric fossa, the features that distinguish the skull of *Tremarctos* from the skull of *Ursus*, although much less exaggerated, are similar to the features that distinguish the skull of the

giant panda (*Ailuropoda*)'. Kurtén (1967) mentioned the similarity between the tremarctine *Arctodus* and *Indarctos*.

However, the teeth of the tremarctines are much closer to those of *Ursus* than any other agriotheriine. The P^4 lacks a parastyle and the molars are similar to those of *Ursus*.

Its ancestry may lie with the agriotheriine *Ursavus*, and the problematical (?) *Ursavus pawniensis* Frick 1926 from the North American Miocene may be the ancestral form. Erdbrink (1953) suggested that the tremarctines are not a homogeneous group, and he derived *Tremarctos* from ursine stock, but the 'arctotheres' (*Arctodus*) from *Indarctos*. However, Kurtén (1966: 7) found that although the 'earlier history of *Arctodus* is poorly documented . . . there can be little doubt that it is a tremarctine'.

Another significant characteristic of tremarctines is the entepicondylar foramen of the humerus. This is a feature also present in the humerus of *Indarctos* (e.g. *I. oregonensis*), *Ailuropoda* and the Hemicyoninae from which the Agriotheriinae are derived. It is, however, not present in the humerus of the Ursinae. It is here regarded as a primitive characteristic retained in at least two agriotheriine lineages (*Indarctos*—*Ailuropoda* and ?*Ursavus*—Tremarctini), but lost in the Ursinae and perhaps also the *Indarctos*—*Agriotherium* lineage.

The conclusion reached here is that the tremarctines do belong in the Agriotheriinae, having stemmed from an *Ursavus*-like ancestor, and having paralleled the Ursinae in some respects.

As with *Ailuropoda*, the only surviving tremarctine, *Tremarctos ornatus*, occurs isolated from the Ursinae, in this instance in South America. Both *Ailuropoda* and the tremarctines co-existed with ursines for much of the Pleistocene, and in the case of the tremarctines for part of the Pliocene as well (Bjork 1970), so their inferred replacement by the ursines was a slow process. However, the fact remains that they were definitely in decline by the end of the Pleistocene, whereas the Ursinae were still remarkably successful. But for the advent of human civilization the Agriotheriinae might well have become extinct while the Ursinae might have remained a prominent part of the world's fauna.

Subfamily **Ursinae**

Diagnosis (see Pilgrim 1931).

Discussion. There is an extensive literature on modern and fossil ursids and a substantial proportion is devoted to the Ursinae. It is the best known and least controversial of the ursid subfamilies and only in the case of the sun bear, *Helarctos*, and the sloth bear, *Melursus*, are there any real doubts about ancestry. The subfamily apparently stems from the early Pliocene *Protursus* (Kurtén 1971), and the genera *Ursus* and *Helarctos* are first recorded in the late Pliocene, while *Melursus* is known only from the Quaternary.

Four categories may be distinguished within the subfamily. The first two are the *Helarctos* and *Melursus* groups, both of which are represented by a single

extant species, and in neither case is there a good fossil record. The genus *Ursus* can conveniently be divided into two groups. The first comprises *U. americanus* and *U. thibetanus*, the North American and Asiatic black bears, and the second is the brown bear group, *U. arctos* and related forms. The latter includes the polar and grizzly bears as well as a number of extinct species such as the giant *U. spelaeus*. They are an extremely successful group and at one time or another they have been distributed through much of the Northern Hemisphere, including the Arctic and North Africa.

THE LANGEBAANWEG BEAR

Agriotherium africanum n.sp.

Holotype. A left maxillary fragment with P⁴ (South African Museum No. L 2045).

Referred material. A part of an ulna (L 2154) and isolated teeth as follows:
L 1868A—E: I₃, I₁, ?P³ and parts of P⁴ and M¹.

L 12637: M².

L 1844 & L 3141: I₂ and I₃.

L 12561: M₃.

Locality. All the specimens are from 'E' Quarry, Langebaanweg.

Diagnosis. A species of *Agriotherium* of large size, in which the P⁴ has a prominent parastyle and a well-developed protocone lobe, the latter consisting of the protocone, an antero-internal cusp and a small intermediately situated cusp; the protocone lobe projects and is flattened posteriorly where it functions as a shearing surface additional to that of the paracone and metastyle. The M² is smaller than M¹ and is without a talon. The antero-buccal surface of M₃ is inflated.

Etymology. The specific name is given in recognition of the fact that this is the first agriotheriine recorded from Africa.

DESCRIPTION

Only two of the specimens, the ?P³ and M₃ are complete in all respects, while the referred P⁴, M¹ and M² are so poorly preserved that not a single standard measurement could be taken on them. The latter are important, however, since they do give an indication of the morphology of the teeth concerned. In general the Agriotheriinae are not well represented in the fossil record, but the Langebaanweg species can be less adequately defined than most of the recorded species of the subfamily.

The ?P³ (L 1868C) (Plate 19 F, G) is referred to this species since it was found in association with the other L 1868 specimens, which unquestionably do belong to *Agriotherium*. In size (10,8 × 7,8) it is comparable to the P³ of an *Indarctos atticus* specimen described by Thenius (1959b), and it resembles this

tooth in being broadest anteriorly. It is a simple, low-crowned tooth with a barely perceptible principal cusp from which arise keels, one running posteriorly and the other antero-internally. The crown is supported by a single antero-posteriorly elongated root.

The carnassial fragment L 1868D is incomplete, but what remains matches corresponding parts of the holotype P⁴ (Plate 19 A-E). This tooth differs in some respects from those of previously described specimens of *Agriotherium* and *Indarctos*, although in size (Table 2) and general appearance it is similar to the P⁴ of these genera.

TABLE 2. Dimensions of the P⁴ of some species of *Agriotherium*

| | <i>A. insigne</i> France (1) | <i>A. sp.</i> Spain (1) | <i>A. palaeindicus</i> India (2) | <i>A. sivalensis</i> India (2) |
|---------------|------------------------------------|-------------------------------|--|--------------------------------------|
| length . . . | 29,1 | 30,0 | 28,0 | 33,0 |
| breadth . . . | 21,0 | 23,0 | 21,0 | 19,8 |

| | <i>A. gregoryi</i> N. America (1) | | | <i>A. africanum</i> South Africa |
|---------------|---|----------|-----------|-------------------------------------|
| | UC 24027 | UC 24025 | AM 18121A | L 2045 |
| length . . . | 23,3 | 35,4 | 36,5 | 32,5 |
| breadth . . . | 21,7 | 25,8 | 25,0 | 25,5 |

(1) Frick (1926)

(2) Lydekker (1884)

The crown consists of a parastyle, which is damaged, paracone and metastyle, which are flanked lingually by a large protocone lobe made up of a protocone, antero-internal cusp and a small, intermediately situated cusp. There are two roots on the buccal side of the tooth and another supporting the protocone lobe. Although the parastyle is damaged, sufficient remains to indicate that it was large and made up about 25% of the total length of the tooth. In this respect it is typical of the P⁴ of *Agriotherium* in which the parastyle is always large, whereas in *Indarctos* it is usually not as well developed. The paracone and metastyle are approximately equal in length and make up the remaining 75% of the total length of the tooth. Shear facets have been worn on the lingual surfaces of these cusps.

The Langebaanweg P⁴ differs most markedly from previously described *Agriotherium* and *Indarctos* carnassials in the size and morphology of the protocone lobe. Its length (22,5 mm) can be measured accurately since its anterior

and posterior limits are clearly defined. In most other Agriotheriinae this is not the case as the posterior limit of the protocone merges gradually with the lingual surface of the metastyle, but in any case they all have shorter protocone lobes. In addition, the protocone lobe of L 2045 differs from other species of *Agriotherium* in that it has a fairly prominent antero-internal cusp, although this cusp is present in *Indarctos*. It is small in *I. punjabiensis*,* but quite large in *I. lagrelli* (Zdansky 1924) and *I. atticus* (Thenius 1959b).

The protocone itself is unique in that instead of being conical, it has its apex elongated antero-posteriorly and compressed towards the paracone and metastyle. The elongation of the protocone lobe as a whole is largely due to the shape of the protocone. The functional advantage of this elongation is readily evident, since the posterior part of the protocone has developed on it a shear facet which is supplementary to that of the paracone and metastyle. Of all the *Indarctos* and *Agriotherium* upper carnassials presently known, that of the Langebaanweg species seems the best adapted to a shearing function.

Another unusual feature of the protocone lobe is the small cusp situated between the antero-internal cusp and the protocone. The cusp itself has been all but worn away, but its presence is marked by a circular patch of exposed dentine. It, and the most anterior part of the protocone have almost horizontal wear facets, indicating that the P⁴ served a crushing function as well.

Parts of the enamel of this tooth show the 'wrinkling' or rugosity said to be characteristic of *Agriotherium* (Erdbrink 1953).

In its general morphology the P⁴ of the Langebaanweg species is not dissimilar to that of *Ailuropoda*.

A small part of the maxilla of the holotype is preserved. The most anterior part of the alveolus of M¹, and part of the antero-external root of this tooth are present. The M¹ must have had a transverse diameter of at least 30 mm, which is in keeping with the size of this tooth in *Agriotherium* and *Indarctos*. The inferior margin of the infra-orbital foramen is also present and it is situated above and slightly posterior to the P⁴.

Little of the M¹ (L 1868E) is preserved. Parts of the roots supporting the paracone and protocone are present, and that root beneath the protocone is large, antero-posteriorly elongated and inserted at an angle to the plane of the palate. The other preserved root is smaller, transversely elongated and inserted vertically into the maxilla. It presumably matched the now missing root which supported the metastyle. Most of the crown is lost and the only enamel preserved is near the paracone. Judging from the preserved parts of the crown and the roots, this tooth appears to have been narrower lingually. The transverse diameter is estimated to have been 30 mm, which is comparable to the figure inferred for the missing M¹ of the holotype. The antero-posterior diameter must also have been about 30 mm.

* This cusp was shown in Lydekker's (1884) illustration, but others (e.g. Matthew 1929) apparently overlooked it.

The M^2 (L 12637) is an important specimen, since although it is incomplete, its morphology indicates that the affinities of the Langebaanweg agriotheriine lie with *Agriotherium* rather than *Indarctos*. It consists of a paracone and metastyle which are equal in size, situated parallel to a protocone and hypocone which are also similar in size. The latter cusps are lower than the paracone and metastyle. The enlarged and posteriorly elongated talon which characterizes the M^2 of *Indarctos* is not in evidence. This tooth is appreciably smaller than the M^1 and its dimensions are estimated to be 25×25 mm. It is thus smaller than the M^2 of previously described species of *Agriotherium* (see Frick 1926: 81).

A reconstruction of the posterior upper dentition of the Langebaanweg agriotheriine is illustrated in Figure 2.

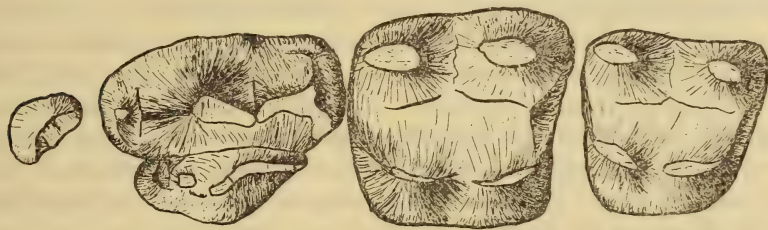


FIG. 2. A reconstruction of the posterior upper dentition of *Agriotherium africanum* based on the specimens L 1868C, L 2045, L 1868E and L 12637 (Natural size).

Little can be said of the lower incisors which are preserved (L 1868A, B, L 1844, L 3141) (Plate 20 A) other than that they are large and agree in all morphological respects with the corresponding teeth of *Indarctos lagrelli* (Zdan-sky 1924) and an *Indarctos* specimen from Samos (Helbing 1932). No descriptions or illustrations of the lower incisors of *Agriotherium* could be located, but presumably they are essentially the same as those of *Indarctos*.

The M_3 (L 12561) (Plate 20 B) is a single-rooted and low-crowned tooth with an almost circular and flat occlusal surface. The antero-buccal part of the crown is inflated and there is a wear facet in this region angled from the occlusal surface across the inflation towards the cingulum. This presumably results from occlusion with the lingual surface of the paracone or metastyle of M^2 . This is an indication that the post-carnassial teeth of this species functioned as shearing as well as crushing agents. The M_3 measures $16,5 \times 16,9$ mm.

The ulna (L 2154) (Plate 20 C, D), which lacks the distal end, lower part of the shaft and anconeus process, is far too large to be confused with the ulna of any other carnivore species in the Langebaanweg assemblage. It compares closely in size (Table 3) and morphology with the ulna from Pikermi referred to *Indarctos atticus* by Pilgrim (1931).

TABLE 3. Dimensions of the Langebaanweg *Agriotherium* ulna, compared with that of an *Indarctos* (?) cf. *atticus* specimen from Pikermi (Pilgrim, 1931).

| | L 2154 | Pikermi |
|---|--------|---------|
| Dorso-ventral diam. at coronoid process . . . | 87,0 | 85,0 |
| Transverse diam. at coronoid process . . . | 59,0 | 61,0 |
| Transverse diam. at proximal end . . . | 50,0 | 52,0 |

DISCUSSION

The genera *Agriotherium* and *Indarctos* share many dental and osteological characteristics, but it is clear that the Langebaanweg agriotheriine has greater affinities to the former genus. It is regarded as a species distinct from those previously recorded since it exhibits certain apparently unique characteristics, and in addition it is the most geographically isolated record of the genus.

Agriotherium africanum differs from previously described species in the size of M^2 and in the nature of its P^4 and M_3 . All the species of *Agriotherium* are known from single, or perhaps a few individuals and it has therefore not been possible to assess the range of variation in any of them. However, R. H. Tedford (pers. comm.) has found 'considerable variation [in the P^4] within and among populations of Hemphillian *Agriotherium* from the United States', although none of the North American specimens matched the *A. africanum* P^4 . If the Langebaanweg species is conspecific with a known species, then it is likely that it would be one of the Eurasian forms, which presumably also had variable upper carnassials.

In this connection the geographical location of *A. africanum* is probably significant. Of the 18 species of fissiped carnivores known from Langebaanweg, only four have affinities with contemporary Eurasian species. Much the same applies to the non-carnivorous mammals. Consequently it is probable that although there is a general similarity between the late Pliocene mammal faunas of Eurasia and Africa, each area was represented by its own lineages. For example, although the Langebaanweg *Percrocuta* is fairly similar to the Eurasian *P. eximia*, it is sufficiently different to warrant the status of a separate species. Similarly the boselaphine from Langebaanweg resembles *Tragoportax salmontanus* from the Siwaliks of India, but the two are clearly not conspecific.

Even if larger numbers of individuals of the Eurasian species of *Agriotherium* become available in the future, it seems unlikely material matching that from Langebaanweg will be recorded. It was on this basis that the decision was made to refer the Langebaanweg *Agriotherium* to a new species.

Probably it is just a matter of time before more agriotheriine remains are recovered elsewhere in Africa, especially in view of the attention presently being focused on Pliocene deposits in East Africa. It is also possible that more material of *A. africanum* will be found at Langebaanweg, since some of the deposits from which present specimens were derived remain unexcavated. Consequently more adequate definition of *A. africanum* might still be possible, and its phyletic relationships might yet be more accurately determined.

SUMMARY

An account of the family Ursidae (Mammalia: Carnivora) is given and a new ursid species, *Agriotherium africanum*, is described.

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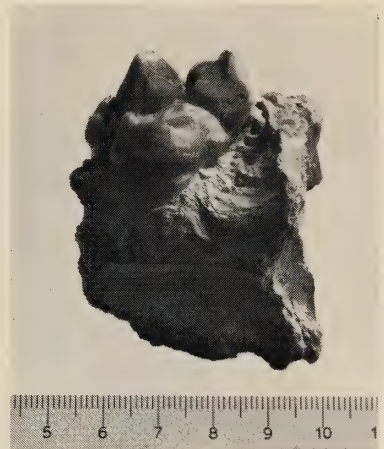
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A



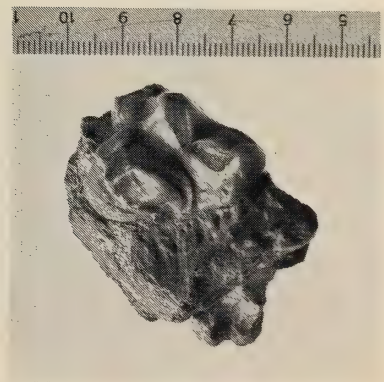
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D



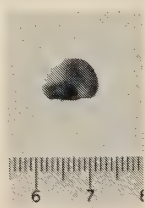
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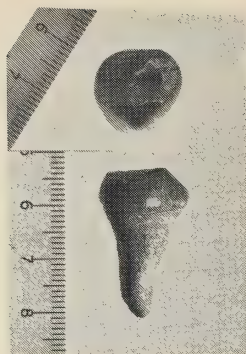


G

A-E Buccal, anterior, occlusal, lingual and oblique views of the *Agriotherium africanum* holotype L 2045.
F & G Lingual and occlusal views of the ?P³ of *Agriotherium africanum* L 1868C.



A



B



C

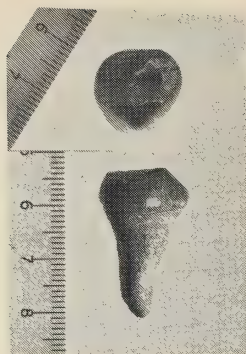


D

A Lingual view of the I_3 of *Agriotherium africanum* L 3141 and L 1868A.
 B Occlusal and posterior views of the M_3 of *Agriotherium africanum* L 12561.
 C & D Anterior and medial views of the ulna of *Agriotherium africanum* L 2154.



A



B



C



D

A Lingual view of the I_3 of *Agriotherium africanum* L 3141 and L 1868A.
 B Occlusal and posterior views of the M_3 of *Agriotherium africanum* L 12561.
 C & D Anterior and medial views of the ulna of *Agriotherium africanum* L 2154.